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# THE DEVELOPMENT OF THE SPORANGIUM OF LYGODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY, 101

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(WITH THIRTY-SEVEN FIGURES)

In his "Studies in the morphology of spore-producing members" (No. IV), BOWER suggests a line of evolution from the Marattiaceae to the Polypodiaceae, with the Osmundaceae, Schizaeaceae, Gleicheniaceae, Cyatheaceae, Hymenophyllaceae, and related forms as representatives of intermediate types. The Marattiaceae and Polypodiaceae are well-worked groups, but the intermediate forms are not so well known. *Lygodium*, one of the Schizaeaceae, has been chosen, therefore, for the present study.

In his classical work on this family, PRANTL<sup>1</sup> considered the morphology and the taxonomy of the whole family. His description of the sporangium of *Lygodium* is here verified except in one point, which will be mentioned later. The present work calls attention to some points that have not been noted in other studies and emphasizes some that have been quite neglected.

The material of the present study came from the Philippine Islands and was collected by Dr. H. N. WHITFORD on Mount Mari-veles, Province of Bataan, Luzon, and was sent to the University of Chicago for demonstration purposes. The species described in the paper is *L. circinatum*; but *L. flexuosum* was also examined and found to be somewhat less variable.

ARRANGEMENT AND ORDER OF SPORANGIA.—The sporangia are in two rows on the ventral surface of the fertile lacinia, and are solitary, i. e., there is only one sporangium in a sorus; PRANTL calls this a "monangial" sorus. The indusium grows out around the sporangium so as to form a pocket open toward the apex on the ventral side

<sup>1</sup> Untersuchungen zur Morphologie der Gefässkryptogamen. 2. Heft. Die Schizaeaceen, morphologisch und systematisch bearbeitet. Leipzig. 1881.

of the leaf (*figs. 1, 2*). The sporangia arise in acropetal succession on the margin of the lacinia (*fig. 3*). The initial cell of the sporangium appears as a marginal cell near the apex of the pinnule; and at first it projects obliquely outward and forward. The indusium arises from the edge and ventral surface of the pinnule basal to the sporan-

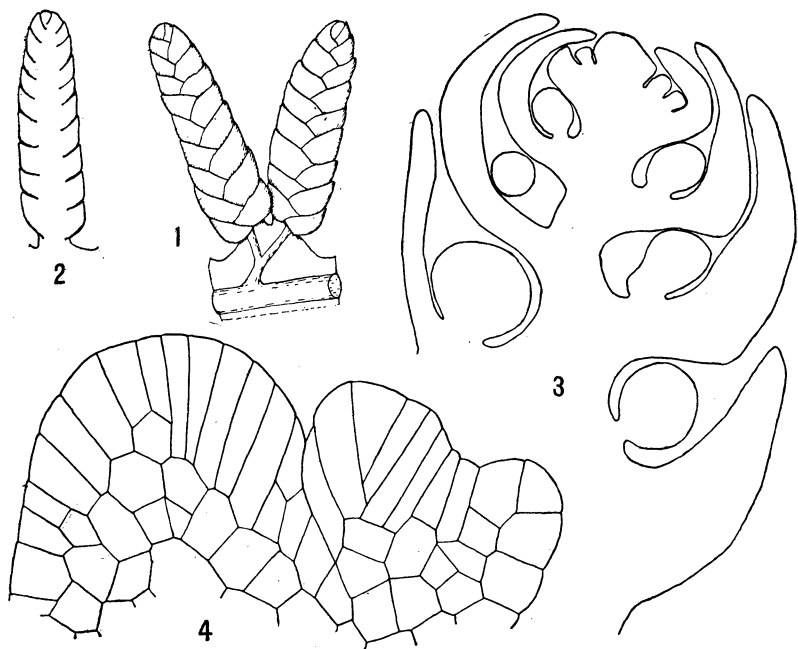


FIG. 1. Two pinnules bearing sporangia (ventral surface).  $\times 13$ .—FIG. 2. Dorsal surface of a pinnule.  $\times 13$ .—FIG. 3. A longitudinal section of a pinnule showing the sporangia.—FIG. 4. A longitudinal section of a pinnule showing the apex and an early stage in the development of a sporangium and indusium.

gium (*fig. 4*). The growth of the indusium out from the edge of the pinnule carries the base of the sporangium out, as shown in *fig. 3*, so that it projects forward or slightly in toward the costa. The part of the indusium which arises from the ventral surface grows out and forward so as to cover the sporangium on the ventral side, but on the dorsal side it is exposed for some time (*figs. 5, 6*). Later a forward growth of lamina incloses the sporangium (*fig. 3*), and carries its base forward so that it projects in a ventral direction. It has thus been

shifted from a marginal to a ventral position, and finally stands at nearly a right angle to the plane of the lacinia.

As stated above, the initial cell of the sporangium appears near the apex of a fertile portion of the leaf (*figs. 7, 8, 9*). A part of one of the segments of the apical cell enlarges and an oblique wall cuts in, either

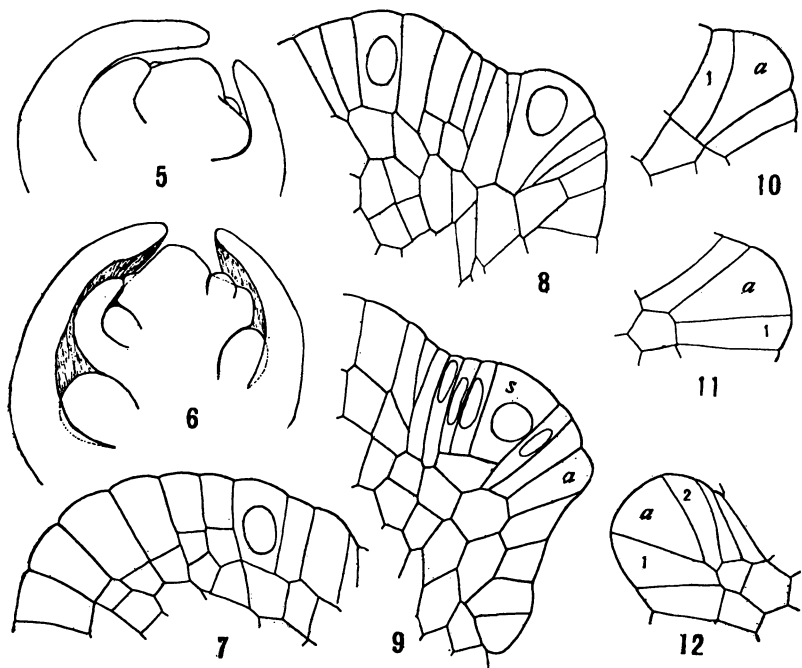


FIG. 5. The ventral side of a pinnule showing the sporangia are soon covered by the indusium.  $\times 130$ .—FIG. 6. The dorsal side of a pinnule showing the sporangia not covered by the indusium.  $\times 190$ .—FIG. 7. The apex of a pinnule showing an initial sporangial cell.  $\times 980$ .—FIG. 8. A longitudinal section of a pinnule showing the apical cell and a sporangial initial.—FIG. 9. An initial cell, *s*; and the beginning of the indusium, *a*.—FIG. 10. The first division of the initial cell, the first wall coming in on the anterior side. *a*, initial cell; 1, first cell cut off.  $\times 980$ .—FIG. 11. The first division of the initial cell, the first wall coming in on the basal side.  $\times 980$ .—FIG. 12. A section showing the first and second cells cut off from the initial cell.  $\times 980$ .

from the front or back, as shown in *figs. 10* and *11*. A second wall comes in on the opposite side from the first and at its lower edge sets upon the first (*fig. 12*); the third wall is parallel with the first and sets upon the second (*figs. 13, 14*), showing a dolabrately apical cell.<sup>2</sup> These

<sup>2</sup>I use the term proposed by Professor BARNES as an equivalent of the German *zwei-schneidige*, instead of the unfortunate translation "two-sided."

walls are usually at right angles to the plane of the leaf. These divisions, which are peculiar ones in the ontogeny of a sporangium,

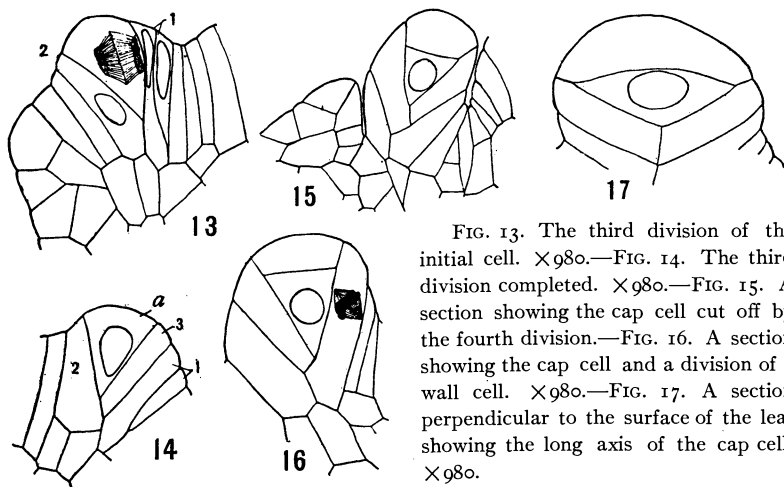


FIG. 13. The third division of the initial cell.  $\times 980$ .—FIG. 14. The third division completed.  $\times 980$ .—FIG. 15. A section showing the cap cell cut off by the fourth division.—FIG. 16. A section showing the cap cell and a division of a wall cell.  $\times 980$ .—FIG. 17. A section perpendicular to the surface of the leaf showing the long axis of the cap cell.  $\times 980$ .

may be the result of the marginal initial cell. This question naturally arises: Is the position of this cell such that the conditions which determine the direction of walls cannot produce the usual tetrahedral form? I know of no other fern which has the sporangia arising on the margin of a

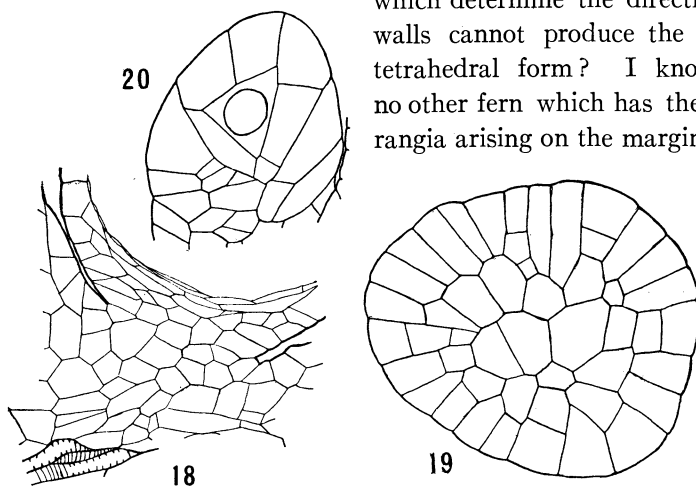


FIG. 18. A longitudinal section of the stalk of the sporangium showing the stalk to be very short.—FIG. 19. A cross-section of the stalk.  $\times 980$ .—FIG. 20. A section of a sporangium showing the early division walls of the stalk and wall cells.

layer of tissue one cell thick. I found one instance in which the walls were not at right angles to the lamina of the pinnule.

The fourth division cuts off the cap cell (*figs. 15, 16*), which in longitudinal section perpendicular to the leaf surface appears as an arch over the central cell (*fig. 17*). This is the longest axis of the cap cell.

**THE STALK.**—The stalk is short and thick (*figs. 18, 19*), the first

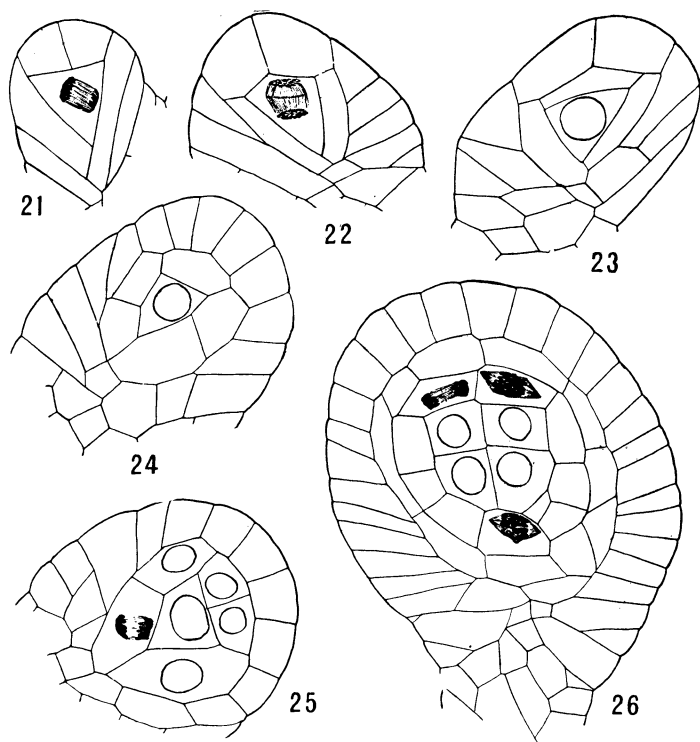


FIG. 21. The first division of the central cell.  $\times 980$ .—FIG. 22. The third division of the central cell to form the third tapetal cell.  $\times 980$ .—FIG. 23. The young sporangium after the three tapetal cells have been cut off.—FIG. 24. Anticlinal walls in the tapetum.—FIG. 25. The first periclinal division in the tapetum.—FIG. 26. A later stage in the development of the tapetum.

cells cut off from the sporangium initial dividing first by anticlinal and then by periclinal walls to supply its cells (*figs. 16, 20*). *Fig. 20* shows that the adjoining cells also contribute to the stalk.

**THE TAPETUM.**—The tapetum is cut off from the three convex surfaces of the central cell (*figs. 21, 22, 23*); the cells divide by anticlinal

(fig. 24) and then by periclinal walls (figs. 25, 26), making a many-celled tapetum of two layers (fig. 27). It is not always definitely two layered, as shown in figs. 28 and 29.

When the sporogenous tissue has reached the mother-cell stage, or somewhat before, the inner layer of tapetal cells becomes greatly enlarged (fig. 29), while the wall of the sporangium rapidly increases in size. Many of the cells of the tapetum become binucleate during this period and the nuclei are together in the end next to the sporogenous cells. Finally the inner layer of the tapetum is disorganized and the cytoplasm flows in around the spore mother cells (fig. 30).

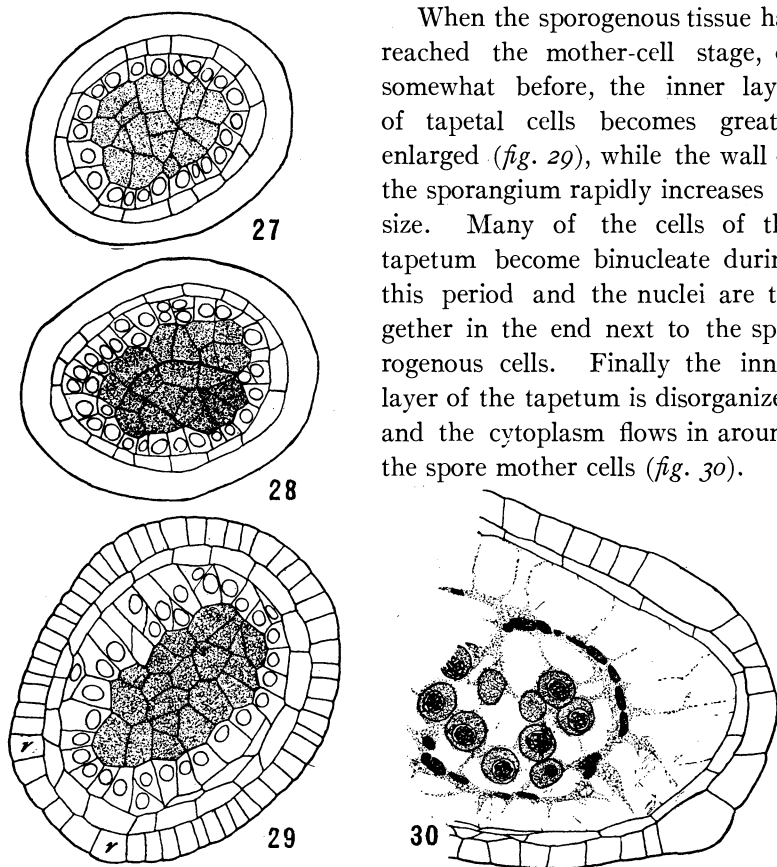


FIG. 27. A section of the sporangium showing the sporogenous mass and the two-layered tapetum.  $\times 480$ .—FIG. 28. A section of the sporangium showing a doubling of the inner tapetal layer.  $\times 480$ .—FIG. 29. A section showing a further development of the inner tapetal layer and the beginning of the annulus, *r, r*.  $\times 480$ .—FIG. 30. The spore mother cell stage of the sporangium and the breaking down of the tapetum.  $\times 480$ .

This development of the tapetum seems to be related to a rather large sporogenous mass where nutrition is difficult. The order of events is as follows: first a comparatively small amount of growth

in the sporogenous mass up to the mother-cell stage, and then a large growth of the sporangium wall. When the spore mother cells have rounded off and the tapetum has entered in between them, conditions are good for the growth of these cells and the spores, which then grow rapidly. Thus we have an alternating growth between the sporangium wall and the spores, which relieves the nutritive strain.

**THE WALL.**—The outer wall of the sporangium is formed mostly from the cap cell (*figs. 31, 32*). The first wall formed in the cap cell

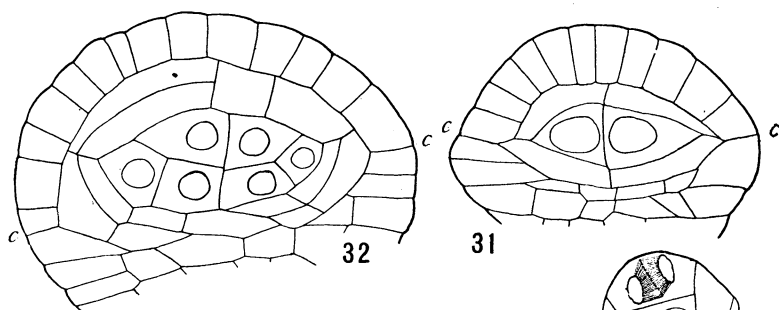


FIG. 31. A section showing the cells derived from the cap cell arched over the sporangium from *c* to *c*.  $\times 980$ .—FIG. 32. A section of a sporangium somewhat older than the one shown in *fig. 31*.  $\times 980$ .—FIG. 33. A section of a sporangium, cut parallel with the surface of the leaf, showing the first division of the cap cell.  $\times 980$ .

is said by PRANTL to be parallel with the leaf surface, but I find that its position varies. *Fig. 33* is from a section cut parallel with the leaf surface and it is here seen that the first wall is perpendicular to plane of the lamina.

The annulus appears as a circle of cells, one to three cells wide, on the costal side of the sporangium (*figs. 29, 30*). These cells become much elongated in the direction of their axes, which are parallel with the sporangium wall and with the cell walls which separate them one from the other. This development gives the sporangium a beaked appearance. The ring is widest on the upper side, where the thick-walled cells of the annulus extend out along the sides of the stomium, which is perpendicular to the annulus and in the median plane of the sporangium. On the upper side the ring is three cells wide; on

the under side it is only one cell wide. In this species the length of the annulus cells varies somewhat, so that the line which is the border of the ring is rather irregular.

The number of wall cells included within the annulus at the apical end is twelve to seventeen.

**THE SPOROGENOUS MASS.**—The first division wall of the arche-sporium is usually perpendicular to the longest axis of the central cell (*fig. 31*), which is at first perpendicular to the leaf surface. Other divisions are quite irregular, but some appear curved and parallel with the first walls of the initial sporangial cell (*fig. 28*). The outline of the sporogenous mass becomes very irregular (*figs. 27, 28, 29*), and the tapetal cells thus dip down into it; this makes possible a better nourishment of the sporogenous mass.

The sporogenous mass is rather large and made up of large cells; I have counted as many as seventy-two mother cells, but sixty-four seems to be the usual number. The number of spores per sporangium is 242 to 258 by actual count. Some of the mother cells become sterilized and function as nutritive cells (*fig. 34*). The mother cells and newly formed tetrads occupy but a small portion of the cavity of the sporangium (*fig. 30*). After the spores are formed there is a great increase in their size, so that they finally fill the large sporangium. The average diameter of the spore mother cell, newly formed tetrad, and mature spore are respectively 0.025<sup>mm</sup>, 0.028<sup>mm</sup>, and 0.075<sup>mm</sup>. Occasionally a dwarf spore is found.

**STERILE SPORANGIA.**—The growth of the spores is apparently a great drain upon the pinnae, so great that the young sporangia at the apex are drawn upon for nutriment, and the sporogenous mass in these sporangia is arrested in its development. They contain no cells which take the stain in the manner characteristic of sporogenous tissue; but the cytoplasm takes on a very loose fibrillar structure and there is little material in the cell that stains at all. The outer layer of the tapetum, which usually remains a thin layer of tabular cells, takes on a very great development, the cells bulging into the cavity of the sporangium like great haustoria; *figs. 35, 36, and 37* show various stages in this development. The cells of the wall at this time become filled with food material and stain densely.

**RELATIONSHIPS.**—In the evolutionary line from Marattiaceae to

Polypodiaceae, suggested by BOWER, there is a progress from coherent to separate sporangia; from sporangia of definite orientation to those indefinitely oriented; from imbedded to long slender-stalked sporangia; from tapetum indefinite and derived from the tissue sur-

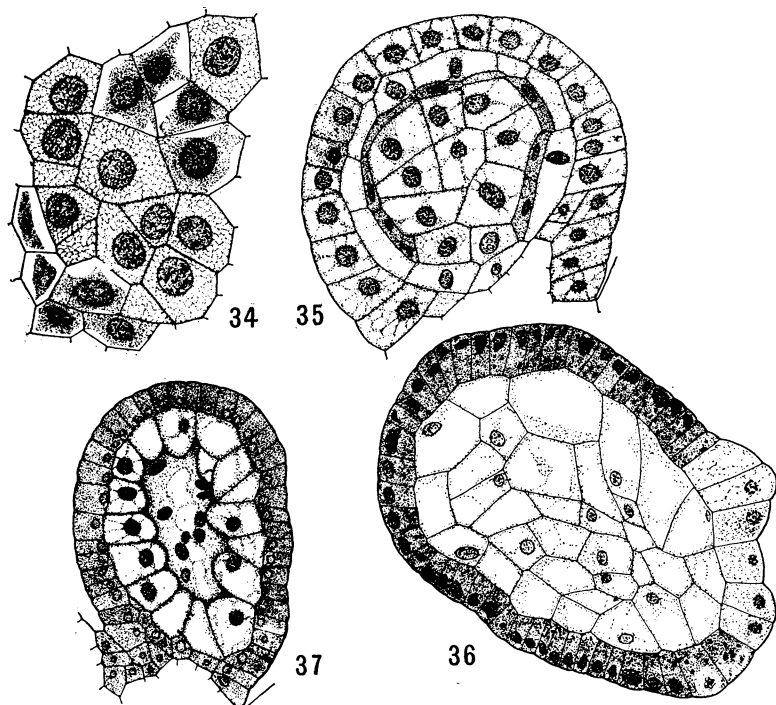


FIG. 34. A section through the sporogenous mass showing some of the cells breaking down.  $\times 980$ .—FIG. 35. A sporangium near the apex of the pinnule; the sporangium is beginning to break down and will not produce spores.  $\times 980$ .—FIG. 36. Another stage in the degeneration of a sporangium near the apex of a pinnule.  $\times 480$ .—FIG. 37. Still another stage in the degeneration of a sporangium near the apex of a pinnule.  $\times 480$

rounding the sporogenous mass to a definite tapetum cut off from the central cell; from no annulus to annulus apical, oblique, and finally vertical; and from indefinite massive sporogenous tissue, not all fertile, but producing many spores, to a small definite sporogenous mass all fertile and producing few spores. In all of these particulars *Lygodium* falls short of the highest polypod type; in all of them also it is above the highest marattiaceous type.

The orientation of the sporangia is definite; this is a characteristic of the lower members of the series. The stalk is shorter and more massive than any other form above *Kaulfussia*. The tapetum is derived from the central cell, as in all the leptosporangiate forms; but the peculiar enlargement of the cells of the inner layer is more characteristic of the lower members of the group. The position of the annulus is the one postulated for the lower leptosporangiate ferns. The large irregular sporogenous mass in which there are occasionally sterile cells, and the large number of spores are also characteristic of the lower leptosporangiate ferns.

The family to which *Lygodium* belongs has some characteristics which cannot be considered as intermediate in this line of evolution, but belong to this family only. The marginal initial cell of the sporangium, whose early divisions are of the dolabrate type, is not reported for any other ferns. The single sporangium in each sorus, the large sporangium and spores, and the indusium, which in cross-section shows the tissue regions of the foliage leaf, are characteristics which in nature or degree of development belong only to this special group of ferns.

In connection with the monangial sorus, BOWER<sup>3</sup> has called attention to the fact that often *Gleichenia* has only one sporangium in a sorus near the apex of the sporophyll. A comparison made by ZEILLER<sup>4</sup> and emphasized by BOWER (*loc. cit.*, p. 43) brings out a close connection between the fossil form *Senftenbergia* and the *Schizaeaceae*, and also connects *Senftenbergia* with the *Osmundaceae* by means of the fossil form *Kidstonia*. *Senftenbergia* is found in lower horizons than most of the marattiaceous ferns, and is the most ancient fern whose sori are well known; these sori are monangial.

*Osmundaceae*, *Kidstonia*, *Senftenbergia*, and *Schizaeaceae* form a series in the development of the annulus, and, as BOWER (*loc. cit.*) has pointed out, the position of the annulus in *Gleichenia* corresponds in some points to that in the *Schizaeaceae*.

But after all these comparisons are made, the peculiarities mentioned above are so striking and apparently so well established, and

<sup>3</sup> Studies in the morphology of spore-producing members. IV. Phil. Trans. Roy. Soc. London B. 192:33. —.

<sup>4</sup> Bull. Soc. Bot. France 44:95. —

the relations of *Lygodium* so ancient, that we can hardly consider it to be very close to the evolutionary line that leads to the Polypodiaceae. It seems rather to have appeared very early in the evolution of leptosporangiate ferns and to have progressed in a line somewhat divergent from the main line leading to the polypods.

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